



# Why do social insect queens live so long? Approaches to unravel the sociality-aging puzzle

Judith Korb

Social insects are characterized by an apparent reshaping of the fecundity/longevity trade-off with sociality. Currently, we have only sketchy information about the potential underlying causes and mechanisms of aging and senescence which in addition are restricted to few model insect organisms (mainly the fruit fly *Drosophila melanogaster* and the honey bee *Apis mellifera*). How can we gain a more thorough understanding how sociality shapes senescence and the fecundity/longevity trade-off? By reviewing available literature, I propose a comparative approach that offers the opportunity to gain fundamental insights into uncovering the basis for this life history trade-off and its reshaping with sociality.

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## Social insects, a promising avenue for studying senescence: a comparative approach

The reshaping of the longevity/fecundity trade-off seems to be universal for social insects regardless of taxonomic position (see Monroy Kuhn and Korb, in this issue; Heinze, in this issue). This makes social insects promising candidates to look for common underlying causes. To unravel and detect commonalities and lineage specific idiosyncrasies requires a comparative approach. Ideally, such comparative studies are done using the same approaches and techniques across a range of social insect clades that evolved sociality independently. Eusociality evolved once in the cockroach-ancestor of termites [1] and once independently in a wasp-like ancestor in ants [2], and multiple times separately in bees and wasps [3,4]. In addition, the degree of sociality and its complexity differ within lineages [5,6] (Séguret *et al.*, in this issue; Toth *et al.*, in this issue). Even in ants and termites where

all species are eusocial, taxa exist with small colonies in which totipotent workers forego reproduction facultatively (e.g. Ponerine ants or wood-dwelling termites) [7]. This provides independent replicates to test how senescence and the fecundity/longevity trade-off are reshaped with increasing social complexity and division of labor. Such studies should include well-studied solitary insects, such as *D. melanogaster*, as control outgroups. By conducting common set-ups of canonical experiments across taxa, it should be possible to uncover common causes and effects that shape the fecundity/longevity trade-off and underlie senescence.

## Manipulations are necessary

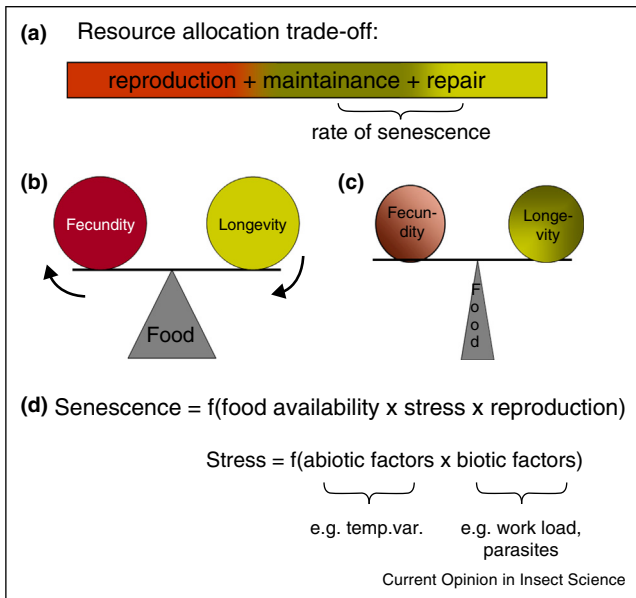
To reveal causal links between fecundity and longevity requires manipulation of the apparent trade-off variables to disentangle their effects in shaping this trade-off (Figure 1). Surprisingly, such experiments have rarely been done [8] and in the model *D. melanogaster* the outcomes have been variable [9]. Manipulations of fecundity are straight forward: An increase in egg-laying rates of females can often be achieved by removal of eggs or offspring. Experiments that aim at decreasing fecundity are equally necessary. Here prevention of egg-laying, for instance, through sterilization of females, is not enough. Instead, one must control for the act of mating itself which may have an effect on longevity as shown for the ant *Cardiocondyla obscurior* [10].

Manipulating the longevity of individuals is more difficult as this can only be done indirectly through variables that are supposed to affect senescence. As shown in preceding papers (Nehring, in this issue, Rodrigues & Flatt, in this issue), these variables are numerous (e.g. oxidative stress, work load, food availability, JH effects) and it is currently unclear which are the most relevant factors, how they interact, and whether they are universal. All these factors can be grouped into three broad categories that are assumed to interact according to the disposable soma theory (Figure 1): stress caused by (i) abiotic factors (e.g. temperature variability), (ii) biotic factors (e.g. work load, social competition, parasites and pathogens) and (iii) food availability. Hence, at least one factor of each category should be manipulated and its impact on the other variables should be quantified to reveal their interactions and the links underlying senescence.

## Output variables

Experiments that aim at testing the fecundity/longevity trade-off require measurements of many output variables. First, manipulations of longevity require quantifications

Figure 1





Fundamental principles of the fecundity/longevity trade-off. (a) According to the disposable soma theory the fecundity/longevity trade-off is largely a resource allocation problem. After reaching maturity, (limited) resources must be allocated optimally between reproduction (fecundity), maintenance and repair processes with the latter two affecting the rate of senescence. (b) In order to show the fecundity/longevity trade-off (or its absence) its variables must be manipulated. If a trade-off exists a change in one variable will affect the other variable. (c) As the trade-off is hypothesized to be a resource allocation problem, food availability must also be manipulated and its effects on fecundity and longevity be quantified. (d) Longevity is difficult to manipulate directly. Senescence is assumed to be a function of food availability, stress and reproduction, where stress can be categorized as abiotic (e.g. due to temperature variability) and biotic stress (e.g. due to work load or parasites). Hence, these variables must be manipulated to test for an effect on longevity.

of their impact on fecundity (and vice versa) (Figure 1). Second, as the proximate causes underlying senescence are unclear and may differ between organisms, a broad range of variables associated with senescence must be studied. To elucidate, for instance, only the importance of oxidative stress, we need to quantify ROS (reactive oxygen species) production, investment into antioxidant defense, and oxidative damage. Quantification of the latter is not enough as low damage may be achieved at high costs that lead to less resources being available for other functions. A straight forward approach here may be to first identify ‘aging markers’ for each study species by comparing old and young individuals, most easily using transcriptome analyses. They can reveal which genes are over/under-expressed in old individuals and whether they belong to certain pathways. Then, the functional involvement of these pathways can be confirmed by more direct approaches, such as measurements of oxidative damage or quantification of hormone titers. Finally, causal links can

be established through manipulations of these variables using genetic techniques such as RNA interference.

Nothing in evolutionary biology makes sense without combining a proximate (mechanistic) with an ultimate (functional) approach [11,12]. All proximate studies that address the mechanistic underpinnings of senescence remain incomplete as long as they do not measure the impact of manipulations on fitness parameters, and finally on lifetime reproductive success. A true trade-off only exists if the experimental change in one traded parameter affects lifetime reproductive success through the other traded parameter. In social insects, testing this requires fitness analyses for all castes and at the colony level (Figure 2). This is not such an easy task as it may appear. First, queens and colonies are long-lived, which makes lifetime measures difficult. Second, also for the shorter-lived worker inclusive fitness calculations can be difficult. In many social insects workers are not sterile and can gain direct fitness [7<sup>\*</sup>] and hence their fitness is not necessarily equivalent with their indirect contribution to colony fitness. This is especially pronounced in species with totipotent workers that only temporarily delay reproduction, such as wasps [13], several Ponerine ants and wood-dwelling termites [7<sup>\*</sup>]. However, workers in many social Hymenoptera with complex societies also have an option to produce male eggs, at least in queen-less colonies [7<sup>\*</sup>]. These direct fitness losses need to be considered when worker longevity is reduced.

Figure 2

Fitness consequences of manipulations					
Outcomes	(a)	(b)	(c)	(d)	
Castes		ns	↓	ns	↓
		ns	ns	↓	↓
Colony	ns	ns / ↓	ns / ↓	ns / ↓	

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Ultimate fitness measures. The impact of manipulations on the fitness of all castes and at the colony level must be quantified. Manipulations may have (a) no fitness consequences for workers, reproductives and at the colony level. They may (b) affect the fitness of reproductives but not those of workers which may or may not have consequences for colony fitness. Alternatively, (c) they may affect the fitness of workers that shield the reproductives from adverse consequences, which may or may not have fitness consequences at the colony level. Finally, (d) fitness of workers and reproductives may be reduced, most likely resulting in reduced fitness at the colony level. Only under (a) there is true absence of a fecundity/longevity trade-off. ns: no significant effect, ↓: reduced fitness.

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